Palaeontology and the Evolution of Man

by

D. M. S. WATSON, F.R.S.
Jodrell Professor of Zoology and Comparative Anatomy in the University of London

The Romanes Lecture

Delivered in the Sheldonian Theatre
4 May 1928

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George John Romanes was remarkable amongst the immediate followers of Darwin in this country for his interest in Scientific Method. In his work he made an attempt to establish the logical basis of his reasoning and to examine the assumptions which had tacitly been made by other exponents of the theory of evolution.

Thus in devoting this lecture to an examination of the methods of palaeontology, so far as they may be applied to the study of man, I feel that I am following a line of investigation which would have been agreeable to its founder.

It is now seventy-two years since the remains of a skeleton found in a cave in the Neanderthal first showed that modern man, *Homo sapiens*, was not a unique phenomenon, that in past time there had lived creatures, men in their qualities of mind, who departed so widely in their bodily structure from all modern races that by the general consent of zoologists they were referred to an extinct species, *Homo neanderthalensis*.

Subsequent discoveries have added four or five other extinct species to the human family, two of which differ so profoundly from one another and from all the remaining forms that special genera, groups of higher order, have been established for their reception.

These human fossils are still so few in number, and their relations to one another both in time and in affinity are so obscure, that their significance can only be

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appreciated by analogy with the much fuller materials which exist for the determination of the history of other mammals.

Palaeontology is an historical science; its importance depends entirely on the fact that its materials are of different date and that their relative ages are known. Thus the first business of a palaeontologist is to determine in geological terms the age of the fossils with which he is working.

In an ultimate analysis our determination of the age of all stratified rocks and of the fossils contained in them depends on the superposition of one bed on another and necessarily pre-existing bed. Such evidence is clearly entirely reliable except in those rare and usually very easily recognizable cases where local occurrences have inverted a series of strata. This orderly arrangement of successive horizons can be determined by direct observation and does not involve any examination of fossils.

The process of geological mapping, depending as it does on an actual or inferred continuity of a bed or formation, is interrupted by areas where rocks of the age under consideration were not deposited or have since been removed or hidden. Thus additional methods have necessarily to be introduced in order to establish the correlation of geological formations in areas far removed from one another.

By the recognition of such purely physical events as an ice age or widespread mountain building, it is possible to divide geological time into a small number of periods which can be independently recognized in all continents. But such time-divisions are far too large to fulfil the requirements of palaeontologists. The smaller divisions of geological time established locally by stratigraphical means can only be extended from region to region by the aid of fossils.

The use of fossils for this purpose depends on the fact that successive formations in the same locality contain different assemblages of animals and plants. This fact rests on a basis of observation and can be established with any accuracy required by extended collection of materials and by more detailed comparisons of the animals from different horizons.

Consideration of the geographical distribution of living animals shows that the observed differences between the faunas of two layers of rock may be due either to the evolution which has taken place during the interval of time which separated their deposition, or to geographical changes which will be indicated by differences in the nature of the sediments.

For the purpose of determination of time, changes of the latter type are valueless. By a comparison of the faunas found in rocks of similar physical character but of different ages, and an investigation of the changes of fauna which take place during the same general period in two not too widely separated localities, it is usually possible to find groups of free-swimming animals which were insensitive to modifications in the character of the sea-floor, and thus to discriminate between the effects of time and environment in altering the fauna. By using only these animals it is possible to make a detailed comparison of the geological succession in disconnected areas and to establish by identity of fauna an equivalence in time of definite formations. That the succession of animals with time may be identical in places so far removed as England and Australia is an astonishing fact which goes far to establish the reality of the correlations so established.

Such use of fossils is exactly analogous to that of potsherds as indicators of period by archaeologists. It is purely empirical, not involving in any way the mutual relationships of the animals of which use is made. It rests entirely on a judgement of similarity of form, a judgement which could theoretically, though seldom practically, be replaced by a statistical investigation of measurements.

Thus a geological 'time-scale' has been built up for each great region of the world, and these have been equated with one another, with varying certainty. This time-scale is not expressible in terms of any unit of time; it consists of a linear series of points in past time which can be recognized all over the world, where each is represented by banks of sand or mud, then laid down and now preserved as a definite geological formation. Thus, wherever they have been collected, fossils may be arranged in an order of time.

In general only the skeletons of animals are preserved, sometimes so perfectly that the whole structure can be investigated in as great detail and with as much certainty as that of the corresponding parts of still living animals. More generally, however, imperfection of preservation and technical difficulties render it impossible to gain a full knowledge of the structure of a fossil. This point of an investigation is one at which errors of observation become important. Only long experience will enable a man to decide whether the nature of his material will justify any particular statement about its structure. The only confirmatory test which can be applied is a reinvestigation by another palaeontologist.

The next business of the investigator is to determine the systematic position of his animal.

Taxonomy, the arrangement of animals into groups, does not necessarily involve any idea of evolution or of actual genetic relationship between different animals. It is an expression of morphological resemblances and differences of special kinds.

Two animals, a lion and a domestic cat, which differ very greatly in size, colour, and many other external features, may none the less resemble one another in structure exceedingly closely. In this particular case every muscle and bone, every cusp on a tooth, every convolution of the brain found in one is present also in the other. Such coincidence in structure is recognizable at sight by a child and is what is implied by taxonomists when they state that two animals are closely allied. But a lion is not accurately a magnified copy of a cat, there exist considerable differences of proportion between the two animals. These differences fall into two categories, one explicable by geometrical and mechanical necessities depending on absolute size, the other unexplained but representing innate characters of the two animals.

The ear has to recognize and discriminate between sound-waves over a definite range of frequency, to analyse movements of the head, and to determine its own position with respect to gravity. These functions can be performed independently of size. Thus there is no reason why the internal ear of a lion should be larger than that of a cat. In fact, whilst a lion is about fifty times as heavy as a cat, the volume of its internal ear is only three times as great. The small ear of the lion requires for its use a correspondingly small apparatus in the brain, which thus differs in its proportions from that of a cat and brings about consequential modifications in the architecture of the skull. Thus when we compare the two animals together with the intention of discovering the closeness of the relationship which exists between them, we must, if our conclusions are to be sound, ignore all those proportional differences which can be shown to depend entirely on differences of weight. After these have been excluded there will remain other proportional differences which may have an independent significance.

Perhaps the best illustration of the application of these principles is to be found in that order of Mammals called the Perissodactyla.

The living Asses and Zebras are universally recognized as close relatives of the horses. Their skeletons correspond accurately bone for bone and process for process with that of the horse. They exhibit differences of proportion which can be accounted for by size together with variations of head shape and the spacing of teeth which cannot be correlated with other characters.

In Lower Pliocene times there lived in the northern hemisphere a series of animals which so strongly resemble the living horses that their systematic position cannot be disputed. Even the Chinese labourers who dig up bones belonging to them for sale to pharmacists as 'dragons' teeth' recognize their skulls as those of donkeys.

All these animals possess in each foot two small hoofs, one on each side of that central toe which alone occurs in the modern horses. Here we have a point of difference which depends on the presence of structures absent in later horses.

In the still earlier Upper Miocene times we find a series of animals, recognizable as horses even by the layman, which differ from the members of the succeeding group not only in the proportions of the three toes but also in the absence of certain articulations between the bones of the wrist and ankle which constantly exist in all later horses.

By a continuation of this process of comparison of the whole of the horse-like creatures of any period with those of an immediately antecedent time, it is possible to show that a group of animals, called collectively *Hyracotherium*, is connected by a close series of structurally intermediate stages with the modern horses. Nevertheless the two differ so greatly that Richard Owen, the most experienced osteologist of his time, did not suspect any relationship between them when in 1856 he first described *Hyracotherium*. But a further examination shows that there are certain characters, the architecture of the astragulus or knuckle-bone for example, which, when allowance is made for changes of proportion explicable on mechanical grounds, remain unchanged throughout the whole history of the horse family. These characters exist also in the rhinoceroses and tapirs, whose earliest forerunners are extremely similar to their contemporary *Hyracotherium*.

Such persistent characters are used by palaeontologists as indicators of affinity. A series of animals, whether of the same or different periods, however varied their habits and general structure, which possesses in common even a limited number of these characters which do not alter is held to be a natural group. This conception is legitimate so long as it is recognized that the classification of animals is based entirely on structural characters. In the particular case which I have described the structural differences between the members of the groups of animals from successive stages is so small that the propriety of including them within a single taxonomic unit is not in doubt. Indeed the case for so doing is made even stronger by the fact that the animals included in the horse family at such a period as the Lower Pliocene are not identical, and that individual animals may be found which combine a general structure which is that of their contemporaries with a morphology of some one organ which is widespread in the family at a preceding or succeeding period.

Further discussion of the series of horse-like forms extending in time from the Lower Eocene to the present day, which has been built up by the process which I have described, involves the assumption that all the horses living to-day are the descendants of some of the horses which were living at every earlier period. But, so far as our knowledge goes, all the horses living in Lower Pliocene times differed from all the living horses in characteristic and uniform ways. Thus either the structure of horses has changed by evolution during the period we are considering, or horses of modern structure existed in those times but their remains have escaped discovery either because they were rare or because they lived in regions which have not yet been examined. That the second supposition is most improbable is shown by the fact that at least ten thousand individual Pliocene horses have been collected from many localities in Europe, North Africa, Asia Minor, India, Persia, Mongolia, China, and North America, all of which agree with one another in the particular respects with which we are concerned. We have considerable assurance that at this time no horses existed in the remaining continents of South America and Australia.

The case in favour of the evolutionary explanation is, however, much stronger. Amongst the hundred thousand specimens of fossil horses from all horizons which exist in the museums of the world none has ever been found in rocks of an age at which its occurrence would not be expected from its structural peculiarities.

Thus by inspection of the successive groups of these animals we can obtain a history, or more accurately a chronicle, of the structural changes which have taken place during their evolution. In doing so we make no further assumptions.

The general character of such chronicles is the same whether they relate to horses, to camels, to elephants, or to any other well-known group of mammals. From inspection of them we can draw certain general conclusions about the nature of the evolutionary process.

(*a*) Evolution commonly leads to modifications of structure which proceed steadily with time so that each animal differs from its predecessor as its successor differs from it.

(*b*) The changes in structure so brought about may be, and perhaps generally are, such as to produce greater mechanical fitness for the special mode of life of the animals considered. But in some cases these changes cannot be shown to have any such adaptive significance.

In order to carry these conclusions farther it is necessary to discover persistent characters which will isolate small groups from the totality of horses existing during a period within which two or more successive faunas are known. We have already seen that the groups so discriminated will be true classificatory units, because the process by which we have established them does not differ in principle from that by which we have built up the whole horse family.

Each of these smaller divisions will exhibit an evolutionary history which, whilst conforming in all its main features with that exhibited by the horses as a whole, will present minor peculiarities which justify us in making further generalizations.

(*c*) The evolution of an organ follows the same course in closely related but independent stocks.

(*d*) The stage of evolutionary advance of an organ in two contemporary related animals is not necessarily identical, but the two will not differ widely. The average condition of all the organs of such forms will be similar within narrow limits. This implies that the rate of evolution is similar in closely related stocks, that this rate is limited by the internal conditions of the animal, and that the individual organs possess a partial independence in their evolution.

(*e*) It is probable that small sudden modifications in structure may take place, and that the characters so introduced may persist for long periods and serve for the discrimination of the smaller phyletic groups.

Thus palaeontology can give much information about the nature of the evolutionary process, although from the character of its material it can never serve to elucidate the mechanism which has brought it about.

Only in few cases can the history of a group of animals be established as a material consisting of abundant specimens from each of a close series of geological horizons.

In most cases, as in that of man, only a few individuals are known from each formation, and the story is interrupted by long gaps. Indeed for many animals we are in a position analogous to that of Kovalevski and Huxley with respect to the horse series. These men picked out four animals which possessed persistent characters in common as horse ancestors. From the series so formed they determined the course of evolution of the feet and teeth in the horse family, and their conclusions have since proved to be justified. But we now know that not one of the animals which formed their 'evolutionary' series is really an ancestor of the modern horses, and that three of them are members of aberrant side-lines which diverged widely from the main stem. Thus, from this and many other cases, it appears that the broad outlines of the course of evolutionary change of such organs as limbs and teeth may be discovered from a series of animals which are not actually ancestral to one another, provided that they lie within a group whose members pursued a parallel evolution and are successive in time.

The process is analogous to that which we should use if we regarded the dress and customs of a man's great uncle as an equivalent of those of his real grandfather. The information we obtain is from a contemporary of similar social position and will differ from that we require only in individual peculiarities. Thus for the establishment of an evolutionary series we are able to use materials far sparser than those which would be necessary for the description of a true phylogeny.

From series so made we can investigate the effects which a profound change in habits, such as that from a terrestrial to an aquatic life, produces in the structure of an animal, and can establish the further proposition that an animal stock will retain in its structure features which were introduced in its ancestors as adaptations to a mode of life which it has long abandoned.

Study of the fossil remains of man is rendered difficult by their fragmentary nature, wide geographical separation, and uncertainty of age. Only by systematically applying palaeontological methods to them and by making use of the analogy of other mammals is it possible to reach any conclusions about their mutual relationships and the course of evolution within the human family.

Perhaps the oldest, and certainly the most primitive, human bones yet discovered are the skull cap, fragment of jaw, two teeth, and a femur which collectively are called *Pithecanthropus*. These fragments were found in river gravels at Trinil in Java, so widely separated from one another that there can be no evidence that they ever formed part of one individual, or indeed that they belong to the same species. The age of the deposits in which they were found can only be established through the evidence of the associated animals and plants, and as the chronology of the Indian rocks which afford the only direct term of comparison is itself uncertain, we are still without definite knowledge of the relative ages of *Pithecanthropus* and other early men.

The famous remains from Piltdown which constitute the genus *Eoanthropus* belong to two individuals found about a mile apart in the same sheet of gravel. This formation cannot be correlated with other Pleistocene deposits by stratigraphical methods. Many of the fossils associated with the human remains are so fragmentary and water-worn that it is most probable that they have been washed out from some earlier deposits and hence give no evidence as to the age of the human bones.

The Heidelberg jaw was found in sands at Mauer, whose early Pleistocene age is well established.

It is commonly believed on real though inadequate evidence that these three human types are of nearly the same age, and that they antedate all other men. By comparing them together we should, on the analogy of other fossil mammals, be able to discover the characteristic structure of early pleistocene man, and by comparison of this with modern races determine the direction of the evolutionary changes of man's structure.

The results of such a comparison are at first very disappointing. One of the most striking peculiarities of *Pithecanthropus* is the immense size of the bony eyebrow ridges. This feature was at first universally regarded as a primitive one, a stage in the gradual refinement of the human face from an anthropoid gorilla-like ancestor. But *Eoanthropus* has supraciliary ridges no larger than those of many living Europeans and in no way supports the older conclusions.

The lower jaw of *Eoanthropus* is so similar to that of a chimpanzee that many anatomists have, mistakenly, denied the possibility of its articulation with the undeniably human skull. It also seems to point to a gorilla-like ancestry. But the lower jaw, which is all that is known of *Homo heidelbergensis*, makes no approach to an anthropoid structure; though immensely massive, and lacking a chin, it is completely human in its dentition and in its plan. It is thus difficult to find features common to the three types which can be regarded as characteristic of early pleistocene men.

The brain of *Pithecanthropus* is, however, far smaller that that of any modern man; in weight it falls almost exactly half-way between the largest gorilla and the smallest Australian. As *Pithecanthropus* seems to have been of ordinary human dimensions, this deficiency in brain exists proportionately. It is in fact associated with a characteristic flattening and lack of development of the anterior end of the cerebral hemispheres.

The brain of *Eoanthropus*, though much larger than that of *Pithecanthropus*, is still small, and it also, as

Professor Elliot Smith has shown, is especially defective in those three regions which are the last to become functional during the individual development of a child. One of these areas is that which overlies the mechanism which is concerned with that symbolical use of sounds which is speech, whilst another from its anatomical relationships is generally believed to be the part of the brain which is concerned with those higher mental faculties which involve the association of ideas.

Thus we find, as we should expect, that there is some direct evidence of that advance in brain structure which must have been the most important part of the evolutionary process which led to modern man.

But our comparison of the three oldest human fossils with one another still leaves us without any certain direction of evolution in the rest of man's structure. Analogy suggests that an investigation of forms of intermediate age should give a clue to the course which the changes have taken.

The only human species which certainly lived in the long interval between *Homo heidelbergensis* and *Homo sapiens* is *Homo neanderthalensis*. His structure is completely known from the many bones found in caves from Western Europe to Jerusalem. Over the whole of this area his remains are associated with that flint-working industry which is called Mousterian.

Most of the skeletons of Neanderthal men have been discovered buried in graves in caves, and the association of many implements with such interments is evidence of the existence of religious beliefs amongst these people.

There is definite evidence that the next culture stage in Western Europe, the Aurignacian, is associated with men of modern structure belonging to our own species, *Homo sapiens*.

The skull and fragments of the rest of the skeleton called *Homo rhodesiensis*, which were discovered a few years ago in a cave at Broken Hill, Rhodesia, are of unknown antiquity, but it is at any rate not improbable that they are at least as old as Neanderthal man.

These two species resemble one another in possessing great eyebrow ridges, but they differ in nearly every other particular.

Rhodesian man has a small brain, nearly as primitive in its structure as that of *Eoanthropus*. The brain of Neanderthal man was very large, curiously shaped, and retained some primitive features. In both races the head was carried so that it projected forward from the thick neck, but the mouth and teeth of Rhodesian man are structurally more similar to those of later races than are those of the Neanderthal race.

Rhodesian man had a long straight femur and walked upright like a modern man; Neanderthal man had a short curved femur and walked on the outer edges of his feet, with bowed legs.

Thus once again we find that a comparison between the human remains of a definite time does not lead to any satisfactory conclusion about the course of evolution.

It is, in fact, clear that in these older human species we have an exaggeration of a phenomenon found in other series of fossils, that variability of structure found in allied animals of the same period which, depending on the parallelism of the evolution of an organ in allied stocks and on variations in the rate of such evolution, results in the association in the same individual of organs of different evolutionary stages.

The variability in the case of man is so unusually great that it suggests that man's evolution has taken place far more rapidly than that of such better-known animals as the horse and elephant. Indeed, analogy suggests that all the extinct human species which we have considered belong to side branches detached from that main human stock of which we are the end. But it should be possible to carry the investigation farther by making use of other animals, the Primates, to which man is structurally allied.

It has long been recognized that there is a very great resemblance in structure between man and the giant apes, the Gorilla, Chimpanzee, and Orang. Indeed, the first account of the anatomy of one of them, published by Edward Tyson in 1699, has as its sub-title, 'The Anatomy of a Pygmie compared with that of a Man, an Ape, and a Monkey'. It may now be said that every structure found in man, whether constantly or as an abnormality, can be found in one or other of the anthropoid apes. The structural differences between them are entirely in proportions.

The analogy of more completely known cases justifies us provisionally in regarding the two groups of animals as close blood relations. Thus by comparing the history of the human family with that of the apes we should be able to determine more accurately the direction of evolution in the former and evaluate the significance of the many anomalies it presents. Unfortunately the giant apes are nearly as rarely preserved as fossils as man himself; only a few score teeth and jaws, together with a single femur and humerus, have so far been discovered.

The anthropoid teeth and jaws which have been found in rocks of Miocene age conform essentially to a common pattern, and mostly belonging to the genus *Dryopithecus*. In the parallelism of the straight rows of cheek teeth they agree with their living representatives, but in them the canine teeth never reach the great dimensions to which they attain in adult male gorillas.

The lower molars have a characteristic pattern, from which that of the living forms can readily be derived, indeed it is often clearly visible in gorilla teeth.

The lower jaw of *Eoanthropus* is, although slighter in build, sufficiently like that of a Miocene ape, and the molar teeth which remain in it, though human in the nature of the wear to which they have been subjected, have exactly the *Dryopithecus* pattern. This structure is preserved with greater or less completeness in all the extinct species of man, whilst it has usually completely vanished in modern races. It is, in fact, true that the older human dentitions differ much less from that of *Dryopithecus* than they do from those of the living anthropoids. This is what would be expected if the two stocks be closely allied. The teeth of both men and anthropoids have undergone evolutionary changes since their separation, and thus now differ more from one another than either does from the common ancestor.

Before we can make use of this conclusion it is necessary to investigate the limits of reliability of the evidence of teeth. These limits are best illustrated by the single molar tooth from the Lower Pliocene of Nebrasca, called *Hesperopithecus*.

The group of American palaeontologists who investigated this tooth are from their long experience and sound judgement the most competent judges of such matters. The tooth had been so greatly worn down by mastication that the pattern of the middle of the crown is completely destroyed, and one of the three roots has been broken away. Thus the animal's affinities had to be determined from little but the structure of the periphery of the crown and roots and the general proportions.

The original investigators were able to show that *Hesperopithecus* did not agree in structure with any tooth which had been described, and finding that in the few features which were available it differed less from the upper molars of apes and men than from any other teeth, deliberately reached the conclusion that it had belonged to an unknown extinct ape. This conclusion appeared so improbable on external grounds that many alternatives were suggested by palaeontologists. None of these suggestions has proved to be correct. Recent discoveries have shown conclusively that the famous tooth belongs to a peccary which in respect to this particular tooth differs from all others.

When unworn the tooth could never be confused with an anthropoid, and a microscopical examination of the structure of its enamel would probably have shown its true affinities. It is thus clear that the few characters shown by a much worn tooth may be inadequate for its certain determination. Much more astonishing is the rarity of such confusions; in general a single molar tooth can safely be referred to its proper place amongst the thousands of fossil mammals which have been described. Indeed, experience suggests that we are justified in laying great weight on the resemblance between early human teeth and those of *Dryopithecus*.

The resemblance is such that it is not impossible that *Dryopithecus* is very nearly a human ancestor as well as an ancestor of the living great apes. Unfortunately we know nothing about the brain and limbs of this animal. It is, however, possible to predict some of its characters from those of its descendants.

The giant apes, with the exception of certain gorillas, spend their life in trees, seldom coming down to the ground. Their structure is very perfectly adapted to a special mode of progression. Instead of walking on all fours along the upper surface of branches, as all the lower monkeys do, they hang from a branch and travel hand over hand along it, as a gymnast does along a horizontal ladder. In association with these habits the arms are enormously long, so that a great distance is covered by each swing, and the hands are becoming great hooks by which the animal can safely hang even from a thick branch. In consequence of this elongation of the whole of the fore-limb the thumb appears small, though actually that of a gorilla is as long as that of a man of similar height. As the legs play no part in this mode of locomotion they are short and bowed, so that the soles of the feet can be pressed together in order to clasp a bough on which the animal may be sitting. Thus the proportionate lengths of the limbs in the anthropoid apes, which differ materially from those which are found in the ordinary quadripedal monkeys, are clearly accounted for by their adaptations to the habit of brachiation.

There is, however, another modification which can be attributed to this habit. The lower monkeys have a chest deeper than it is wide, so that the shoulder-blades lie more on the sides than the back of the thorax. In the anthropoids, in order to allow the arms to be held out laterally, the chest is flattened and the scapulas lie on the back as they do in man.

It is certain that the man-like apes have descended from quadripedal animals, because all primitive mammals have such habit. By analogy with better-known phylogenies we may conclude that the Miocene ancestor of the gorilla had shorter arms, and longer legs, than that animal. The fingers were less bent and shorter, whilst the thumb, which is not used in brachiation, was the same size or perhaps even longer; in any case, it will have been larger proportionately to the other fingers. The legs may have been straighter, more like those of lower monkeys, and the femur less flattened and curved.

It is probable that in these smaller ancestors, as in the smaller chimpanzees and gibbons, the eyebrow ridges were less prominent. But the differences in proportion which exist between such a presumed gorilla ancestor and man are far smaller than those between man and the modern apes.

If man be the descendant of brachiating apes we should expect to find in his structure features which can only have arisen as adaptations to such a mode of progression. Man's broad shoulders and shallow chest, designed to ensure the widest possible stretch between the hands, are one such character, and the many anatomical peculiarities which are associated with an upright body can most easily be explained by his descent from brachiating apes.

Thus it seems certain that man has indeed arisen from an ancestral great ape, differing from the modern forms in his less intense brachiating specializations. Man has undergone his own evolution since that period, and the changes which have occurred in his structure are related to habits entirely different to those of the apes. Thus the use of the legs for walking and running will, on the analogy of all other mammals, result in an increase of their length, whilst the arms, freed from all use in progression and devoted to the handling of food and of tools, necessarily become shorter and capable of more accurately adjusted movements. Indeed it is easy to provide a mechanical explanation for all the proportional differences which separate man from an anthropoid ancestor free from great brachiating specializations.

Such an analysis leads us to the view that the smooth forehead and ape-like jaw of *Eoanthropus* and the straight femora of *Pithecanthropus* and Rhodesian man are primitive features derived directly from their ancestors, whilst the human form of the Heidelberg jaw, the great eyebrow ridges of *Pithecanthropus* and of Rhodesian and Neanderthal men, and the flattened and curved femur of the latter are advances produced by an evolution parallel to that which has produced the gorilla.

Thus palaeontologists have been able to develop methods of studying fossil remains whose validity has been confirmed by the verification of predictions. By the application of these methods to the few remains of early man which are available it has been possible to show that man has indeed evolved from an ancestor which also gave rise to the anthropoid apes. The human stock, like that of many other mammals, gave rise to short-lived side branches, whose members exhibited an unbalanced evolution, some of their organs developing more rapidly than in the main stem, whilst others paralleled the giant apes in their evolution and produced structures which have never existed in our own ancestors.

But the bodily differences which separate man from the apes are unimportant in comparison with those between their mental equipments. The doctrine of causality requires us, as scientific men, to believe that these mental differences are an expression of comparable differences in the activities, and hence in the structure, of the brains of the two animals. The brain of man is constructed on exactly the same plan as that of a gorilla, no structure visible to the naked eye or discoverable by the most refined microscopical technique in the one is absent in the other. In the brain, as in the animal's whole structure, the differences are of size and proportion and not of kind. These differences are so small as to be incomparable with those which separate the mental activities of the two animals. But small as they are, they are much greater than those which exist in visible morphology between the brains of a feeble-minded child, incapable of the simplest mathematical operation, and of a great mathematician.

We do not therefore conclude that the activities of a brain do not depend on its morphology, but rather hold that the significant structure is that ordered arrangement of molecules which must exist within every cell of the nervous system. This structure will never be seen by us, but we may hope to determine its nature by the methods of physics and chemistry.

From such comparisons of visible morphological differences in brains with the vastly greater functional differences which may exist between them, we draw the conclusion that, when a certain degree of complexity has been reached, small changes in the ultimate structure of the elements of a brain may lead to changes in mental activity so vast as to be at present inexplicable.

Thus when the brain of a human ancestor had reached an elaboration comparable to that of a gorilla, as an organ for the control of his simple activities, the comparatively minor structural changes which are associated with speech, and unknown invisible changes in the intimate structure of its cells, enabled its possessor to elaborate the rudimentary aesthetic appreciations and thought of the apes into those mental processes which provide the highest and most lasting pleasures of civilized man.

The most fascinating problems of man's evolution thus lie outside the province of the palaeontologist. He is concerned only with such gross morphological facts as the shapes of bones and of the exterior of the brain, whilst those structures whose qualities can alone explain the meaning of man's evolution lie beyond his sight.

It is to the physiologist, and to the chemists, physicists, and mathematicians, whose methods he uses, that we must look for an understanding of the true nature of man's evolution. Only when man's activities can be expressed in terms of physics will the problem of man's origin reach its solution and that adventure of the spirit which is biology come to its close.

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